Modelling food selection by North Sea whiting

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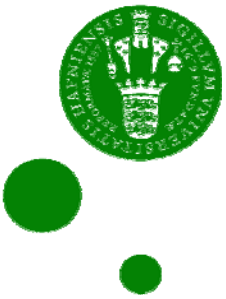

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Danish Institute for Fisheries Research

Department of Marine Fisheries

Preface

The present dissertation is in partial fulfilment of the requirements for obtaining the degree of Doctor of Philosophy (Ph.D.) at the faculty of Natural Science, University of Copenhagen, Denmark. The work providing the basis for the thesis was carried out from 1999 to 2003 while I was employed at the Danish Institute of Fisheries Research. The study was partially founded by a grant from the Danish Ministry of Food, Agriculture and Fisheries to the project 'Development of improved models of fisheries impact on marine fish stocks and ecosystems' (FIFOF-DFU-1) and the Danish Research Academy. The SLIP research school under the Danish Network for Fisheries and Aquaculture Research (www.fishnet.dk) financed by the Danish Ministry for Food, Agriculture and Fisheries and the Danish Agricultural and Veterinary Research Council further supported the project. The data used were collected by Poul Degnbol and Henrik Gislason and I would like to thank them for placing them at my disposal.

I want to thank my supervisors, Henrik Gislason, Peter Lewy and Jan Beyer for their never failing support. They have been as much my friends as my colleagues through this project, and have never turned me down when I needed advise, even when they were very busy doing other things. I also want to thank Morten Vinther, Niels Gerner Andersen, Thomas Kiørboe and Stuart Reeves for valuable comments on my manuscripts, and for spending a lot of time discussing them with me. I could not have had a more supportive and encouraging environment for my thesis. I would further like to thank Anne Gro Salvanes, University of Bergen, Olav Rune Godø, Institute of Marine Research, Bergen, and Ólafur Pálsson, Marine Research Institute, Reykjavík, for letting me visit their institutes, arranging presentations there and for stimulating discussions on food intake and the distribution of fish.

Lastly, I would not have been able to write this thesis without the support of my family. I want to thank my children for taking my mind of the thesis and saving me from spending all my time working, my parents for never failing to step in when called for and my husband for listening to endless accounts of fish and never questioning my decisions to work late or travel.

Copenhagen, December 2003

Anna Rindorf

Summary

This thesis describes an analysis of food intake, functional response and prey selection of whiting feeding on clupeids and small gadoids in the North Sea. Prey fish density was estimated from the average trawl catch of each species, and a new method was proposed to analyse length distributions. Food intake was examined by several different methods. Diel feeding patterns were investigated by analysing changes both in the occurrence of prey in the stomachs and the proportion of prey which was recently ingested. Pronounced diel feeding patterns were found as whiting were feeding on benthic prey at night and on clupeids and gadoids around dawn and dusk. This pattern was consistent at all locations and was most likely linked to diel changes in prey availability. Temporal segregation of different prey types is inconsistent with the assumptions of most food selection models, in which the time used to pursue and ingest one prey is assumed to limit the time available to pursue other prey. Given the observed diel feeding pattern, a negative effect of the amount of night time prey on the amount of daytime prey ingested can only be mediated through satiation of the predator. The effect of satiation on feeding probability and meal size of whiting was studied by comparing the amount of fresh food in the stomachs with the amount of prey in a more advanced stage of digestion. A significant proportion of the whiting were found to be partly or fully satiated, and hence neither complete independence nor complete exclusiveness of the intake of fish prey and other prey existed.

Food intake was estimated by combining knowledge of stomach content with stomach evacuation rates using a new method which takes the difference in evacuation rate of different prey types into account. Evacuation rates of prey were derived both from the literature and directly from field data. The predator was found to prefer herring prey over sprat at most locations. However, the

preference for herring decreased as the relative abundance of herring increased. This phenomenon is called negative switching and is strongly destabilising in a homogenously mixed system. Further, the intake of fish reached a saturation level well below the digestive capacity of the predator. Negative switching and lack of satiation at high prey densities can be caused by either the inability of some predators to locate prey or by individual differences in preferences. Although it has a highly destabilising effect on prey population dynamics at the local scale, negative switching may still induce large scale stability in a heterogeneous system when combined with the observed lack of aggregative response of the predator to high prey densities.

Dansk sammenfatning (Summary in Danish)

Denne afhandling omhandler en analyse af hvillings fødeoptag og selektion mellem forskellige byttetyper ved forskellige bytte tætheder. Byttet var sild, brisling og små torskefisk, og såvel bytte som rovfisk blev indsamlet ved trawling i Nordsøen. Bytte tætheden blev beregnet ud fra fangstrater af bytte fisk, og en ny metode til at analysere længdefordelinger blev foreslået. Fødeoptaget blev undersøgt på flere måder. Døgn variation i fødeoptaget blev undersøgt ved at notere den andel af maverne, der indeholdt hver bytte type og ved at se på den andel af fisk i maverne, der var spist for nyligt. Det viste sig at hvilling på alle fem lokaliteter spiste bunddyr i løbet af natten mens silde- og torske-fisk næsten udelukkende blev spist omkring solopgang og solnedgang. Hvilling havde altså ikke mulighed for på et givet tidspunkt at vælge mellem f.eks. bunddyr og sild, men derimod mulighed for at vælge mellem bunddyr eller ingenting om natten og fisk eller ingenting ved solopgang. De fleste modeller for selektion mellem to fødetyper kræver at der skal være tale om et valg: Idet fisken vælger at spise et bytte skal den afskære sig fra at fange det andet bytte. Men denne situation vil kun opstå for hvilling hvis den er så mæt efter at have spist bunddyr, at den ved solopgang ikke er i stand til at spise fisk. Effekten af mæthed på fødeoptaget blev derfor undersøgt ved at sammenligne mængden af frisk føde med mængden af mere fordøjet føde i hver enkelt mave. Det viste sig at en betydelig del af hvillingerne var uvillige til at spise noget, så der kan altså være en hæmmende effekt af at have spist bunddyr på tilbøjeligheden til at spise fisk. Der var således hverken fuldstændig uafhængighed eller et fuldstændigt valg mellem bunddyr og fisk.

Føde indtag blev beregnet med en ny metode, der kombinerer viden om indholdet af fiskemaver og mavetømningsrater og samtidig tager højde for forskelle i tømningsrater mellem bytte typer. Estimerede tømningsrater kom

både fra litteraturen og fra direkte observationer af døgnvariation i indholdet i hvillingemaver. Hvillingerne foretrak sild frem for brisling på de fleste lokaliteter, men præferencen var mindre når der var mange sild. Dette kaldes negativ switching og har en stærk destabiliserende effekt på byttepopulationen hvis denne er jævnt fordelt. Desuden nåede optaget af fiskebytte et mætningspunkt langt under det niveau hvor hvillingen ville være begrænset af sin fordøjelsesrate. Negativ switching og det lave mætningsniveau kan enten være et resultat af, at ikke alle hvillinger befandt sig i et område hvor der var meget bytte eller af individuelle forskelle mellem hvillingerne, således at nogle foretrak et bytte mens andre foretrak et andet. Selvom negativ switching i sig selv er destabiliserende for bytte bestanden, kan hvillingens fiskeoptag alligevel lede til stabilitet hvis det kombineres med en manglende tilbøjelighed hos hvillingerne til at opsøge områder med høj byttetæthed, og dette kan være en af årsagerne til bestandene i Nordsøens stabilitet.

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List of original publications

This dissertation is based on the following papers, which will be referred to in the text by their Roman numerals:

I Rindorf, A. and Lewy, P. (2001). Analyses of length and age distributions using continuation- ratio logits. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1141-1152.

II Rindorf, A. (2002). The effect of stomach fullness on food intake of whiting in the North Sea. *Journal of Fish Biology* **61**, 579-593

III Rindorf, A. (2003). Diel feeding pattern of whiting in the North Sea. *Marine Ecology Progress Series* **249**, 265-276

IV Rindorf, A. (2004). Estimation of evacuation rates in the field. Published subsequently in *Journal of Fish Biology, **65**,* 262-281

V Rindorf, A. and Lewy, P. (2004). Estimation of fish consumption by stomach content analysis. Published subsequently in *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 2487-2498

VI Rindorf, A. and Gislason, H. (2005). Functional and aggregative response of North Sea whiting. Published subsequently in *Journal of Experimental Marine Biology and Ecology*, **324**, 1-19

VII Rindorf, A. (Manuscript). Testing prey selection models in a natural environment: prey preference by whiting.

Abstracts of the papers are given from p. 71 onwards.

Introduction

The study of the relationship between consumption by predators and density of their prey is a classical discipline in ecology (Errington 1934, Burnett 1954, Holling 1959b). Far from simply consuming every prey they encounter, most predators eventually reach a point where addition of more prey to the system will not increase the amount of prey consumed (Holling 1965, Colton 1987, Buckel and Stoner 2000). Further, few predators select their prey at random from their surroundings. The majority exhibit a preference for some prey types while other prey are largely ignored (Holling 1959b, Manly et al. 1972, Werner and Hall 1974). The study of both saturation effects and prey preferences of aquatic predators have resulted in an abundant literature, mostly documented by results from laboratory studies under which the predator is presented with one or more prey types under controlled conditions (e.g. Werner and Hall 1974, Colton 1987, Hart and Gill 1993). Few studies have examined food intake and selection in detail in natural marine environments (but see Hahm and Langton 1984, Bannon and Ringler 1986, Prejs et al. 1990, Arhhenius and Hansson 1994). A likely reason for this is the difficulty in estimating both predator consumption and prey density in the wild. Food intake and prey density may further only be correlated at a narrowly defined spatial scale (Rose and Leggett 1990, Horne and Schneider 1994) and several factors such as environmental conditions and mortality risk may affect the response (Werner et al. 1983, Gotceitas 1990, Koski and Johnson 2002, Wennhage 2002). Furthermore, the relationship between prey abundance and food intake is rarely linear and this renders it unlikely that the response of the entire predator population is identical to that of the individual predators (Chesson 1978, Chesson 1984, Abrams and Matsuda 1993). Hence the study of food

intake in relation to prey density has two conceptually different levels: the individual level, which can provide knowledge of the processes involved in food selection, and the population level, which provides little knowledge of processes but gives a direct estimate of population interactions.

Population interactions in aquatic environments have been the focus of a vast number of modelling studies (see, e.g., Bax 1998). Generally, these studies adopt one of a number of commonly used feeding models and the ability of this submodel to describe food intake is rarely tested (Gislason and Helgason 1985, Christensen et al. 2000, Shin and Cury 2001). Some authors have attempted to validate a food intake model within a population model (Rice et al. 1991, Larsen and Gislason 1992), but this is often difficult and the results are not easily interpreted as discrepancies may be caused by inadequate formulations at any level within the model. Other studies have examined food selection models directly (Colton 1987, Chesson 1989). The results suggest that existing models such as the commonly applied multispecies version of Hollings 'disc' equation (Murdoch 1973) often does not describe food intake accurately. Generally, although this model predicts that the predator should exhibit a constant preference for one prey over another, the experiments show a change in preference with prey density (Colton 1987, Chesson 1989, Rindorf et al. 1998). The link between food intake and prey density is of crucial importance to the stability of interacting predator-prey populations (Murdoch 1994, Pelletier 2000), and predictions of population models based on unvalidated feeding models are at best poorly founded and may at worst be unrealistic. In a time where there is an increasing focus on the effects of human activities on the stability and diversity of marine ecosystems (Gislason et al. 2000), there is a need for creating a more solid foundation for predictions of the effect of

changes in predator and prey populations on the dynamics of marine ecosystems.

The objective of this Ph.D. study was to examine the ability of a number of food intake and food selection models to describe the feeding of whiting (*Merlangius merlangus*) on herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and juvenile gadoids (Gadidae) in the North Sea, and if necessary to suggest alternative food selection models. Food intake and selection was investigated by comparing prey density inferred from trawl catches with food consumption by whiting estimated from stomach contents analysis. The study included an examination of the variability of trawl catches and a detailed investigation of the factors which affect either food intake or the estimation of food intake from stomach contents.

Ecology of whiting in the North Sea

Whiting is distributed throughout the North Sea in areas shallower than 200 m (Fig. 1, Daan et al. 1990, Bergstad 1991, Wieland et al. 1998). Juvenile whiting are more coastal in their distribution than their older conspecifics and the preferred depth increases with age (Daan et al. 1990, Wieland et al. 1998). The change in depth distribution coincides with a shift from invertebrate prey (particularly copepods, mysids and krill) towards a diet consisting mostly of fish and larger crustaceans (Gordon 1977, Patterson 1985, Hislop et al. 1991).

Fig. 1. Distribution of whiting (*Merlangius merlangus*). From Muus and Dahlstrøm (1989).

Herring, sprat, sandeel (Ammodytidae) and small gadoids are the most important fish species in the diet, together constituting more than 90% of the fish prey (Patterson 1985, Hislop et al. 1991). Whiting are highly cannibalistic and it is estimated that in one year, whiting consumed as much as 36 500 t of their younger conspecifics in the North Sea, corresponding to about 5% of their intake of fish prey (Hislop et al. 1991).

Whiting mature around the age of 2 and have a prolonged spawning season extending from January to October, though the majority of the eggs are released from February to May (Daan et al. 1990, ICES 2001). The juveniles are initially pelagic and migrate vertically, moving towards the surface at day and to deeper waters during the night (Bromley and Kell 1995). Around the beginning of August, the vertical migration pattern dissolves and the juveniles are distributed throughout most of the water column during the entire diel circle (Bailey 1975, Robb 1981, Bromley and Kell 1995). During autumn, they become progressively more demersal and by January, most of the population is found near the bottom (Gordon 1977). Whiting is commonly referred to as being more loosely attached to the bottom than cod (*Gadus morhua*), and are frequently found both in the pelagic and close to the bottom (Whitehead et al 1984, Pedersen 1999). However, there is no inherent preference for pelagic feeding over demersal feeding in this species (Gjøsæter 1990). Stomach analyses indicate a substantial overlap between the diets of whiting caught in the pelagic and demersal layer and benthic prey is frequently encountered in the stomachs of pelagically caught whiting (Pedersen 1999). Thus, although whiting may be less closely associated with the bottom than many other piscivorous gadoids, there is no evidence to suggest that pelagic and demersal whiting should constitute two separate subpopulations (Paper III, Paper VI).

Estimation of prey density

To link food intake to prey density, it is first of all necessary to obtain an unbiased estimate of prey density at a spatial scale relevant to the predator (Rose and Leggett 1990, Horne and Schneider 1994) as a high density of prey will not affect the predator and vice versa if the two are not spatially co-occurring. The appropriate scale is likely to be somewhere between the perceptive distance of the predator and distance the predator can swim within a reasonable time span. Juvenile whiting have been reported to swim at a speed of 2.5 body lengths per second for hours (Hammer 1994) and would be able to travel a distance of 1 and 1.7 nautical miles hourly at a body length of 20 and 35 cm length, respectively. Assuming that the maximum scale of interest to the predator is one that can be searched within a matter of hours (Horne and Schneider 1994), the need to be able to sample prey densities at a corresponding spatial scale with a high precision arises. In the marine environment, the local density of sessile species and species with a restricted home range can be estimated from samples taken by divers (Hall et al. 1990, Stewart and Jones 2001, Wellenreuther and Connel 2002), whereas active prey can be sampled by traps or stationary nets (Paukert and Fisher 1999, Nielsen et al. 2001, Vining et al. 2001). However, neither of these methods are well suited for estimating the density of highly mobile schooling prey. Such species are often sampled acoustically (Rose and Leggett 1990, Misund 1997, Axelsen et al. 2000). Unfortunately, it is at present impossible to distinguish between species of similar size and behaviour directly from their acoustic reflections (Misund 1997, Horne 2000) and neither is it possible to achieve reliable acoustic estimates of prey abundance near the bottom (Ona and Mitson 1996). Due to these difficulties, trawling remains the most applied method to estimate the abundance and size distribution of demersal fish. It provides indices of

demersal fish density that, if not direct measures of large scale density, at least are reproducible by other ships trawling in the same area (Hjellvik et al. 2002b). Trawling does, however, sample a rather large area as trawl hauls frequently cover a distance of 1.5 to 3.5 nautical miles, corresponding to about 1.5 to 3.5 hours of directional swimming by a 20 cm whiting (Engås and Godø 1989b, Michalsen et al. 1996, Hammer 1994).

Inferring prey density from trawl catches

The trawl catch of fish, T, is a function of four factors: the density of fish in the area, N, the volume trawled, V, the proportion of the fish in the water column which occur in the trawled volume, v, and the proportion of fish in the trawled volume which are actually retained by the trawl, g (Parrish 1963, Fig. 2):

$$T = VvgN$$

The product Vvg, e.g. the proportion of fish in the area which are retained by the trawl, is often termed the catchability, q (e.g. Michalsen et al. 1996, Casey

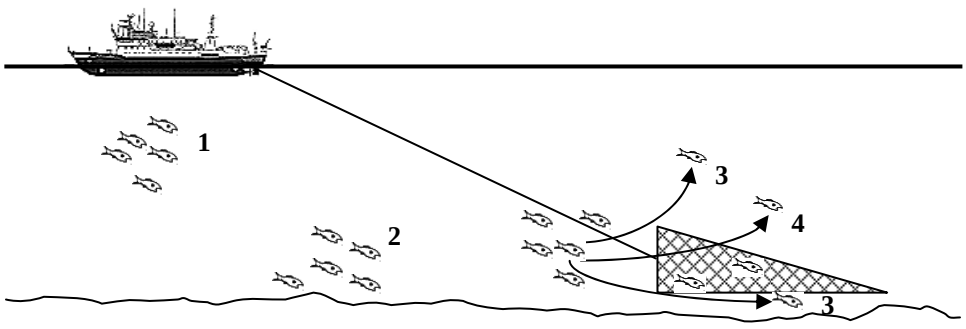

Fig. 2. Factors affecting trawl catchability. Fish distributed above the headline of the trawl (1) are not caught whereas fish distributed in the trawled volume (2) may be caught by the trawl or may escape by passing over, under or around the trawl (3) or through the meshes of the net (4).

and Myers 1998). Though catchability varies with fish species and size (Walsh 1991, Engås and Godø 1989b), it is often assumed to be unaffected by other factors (Quinn and Deriso 1999). This constancy within species size groups has been termed 'the survey condition' and is a prerequisite for the use of trawl surveys to estimate relative density (Godø and Wespestad 1993). A constant catchability makes the trawl catch directly proportional to density and hence a direct index of density. Unfortunately, a number of factors other than fish species and size affect catchability. Catch rates may differ between vessels as a result of differences between vessels or in the rigging of the trawl (Engås and Godø 1989a, Hjellvik et al. 2002b), and even if the same gear and vessel is used, diel vertical migration patterns, light intensity and fish density may affect the catch rate (Michalsen et al. 1996, Casey and Myers 1998, Hjellvik et al. 2002a). A further complication when estimating fish density from survey catches is the uneven distribution of fish over larger areas. Fish tend to be gathered in larger patches with a variable number of individuals in each patch (Rose and Leggett 1990). This structure causes the variability between trawl hauls to increase with density in the area and a significant proportion of the hauls may not contain the particular species at all (Pennington 1983, Stefánsson 1996). This renders the simple average trawl catch a poor estimate of density (Pennington 1983, Smith 1988). Using a particular vessel and gear and trawling the same volume with every haul, the major problems connected to estimating prey density from trawl catches can thus be divided into three: Spatial variation in prey density, diel changes in catchability and the effect of fish density on catchability.

Spatial variability in density

The variability between trawl catches is generally well described by a so called delta distribution (Pennington 1986, Smith 1988, Stefánsson 1996). This distribution combines the probability that a given haul catches any fish at all with a distribution (generally the log-normal- or gamma-distribution) of the catch in weight or numbers in the trawl hauls where fish were caught. The distribution provides minimum variance estimates of catches (Pennington 1986, Smith 1988) and it also allows testing of the significance of e.g. diel differences in catch rates (Stefánsson 1996). If no significant diel difference exists between the catches, the precision of the estimated average trawl catch can be improved by joining all samples, regardless of the time of day at which they were obtained. If, on the other hand, the difference is significant, the unbiased estimates are obtained by treating the samples separately. The need to test for significant differences has led to the development of methods for statistical comparison of length and age distributions (Kimura 1977, Zwanenburg and Smith 1983, Kvist et al. 2001, Paper I). Using such methods, a minimum variance estimate of catch of each species and length group can be obtained.

Diel changes in catchability

Selecting a relevant estimate of density when the trawl catch varies with time of day requires some consideration. First of all, a number of fish species migrate vertically in response to light, current, prey availability or mortality risk (Beamish 1966, Michalsen et al. 1996, Tarling et al. 2000). Secondly, fish are generally more successful at avoiding the trawl during daylight than during darkness (Parrish et al. 1964, Walsh 1991), though the trawl doors, wires,

ground gear and the cloud of suspended sediment raised by these have a visual (daytime) herding effect on some fish species (Main and Sangster 1981, Engås and Godø 1989a). These effects are quite different in their relevance to the predators as the herding and avoidance of trawl gear affects only the trawl catch rate whereas diel vertical migrations may render prey available or unavailable to a predator with a limited vertical range (Harden-Jones and Scholes 1985). Unfortunately it is not possible to separate and quantify the contribution of each effect without additional knowledge of either of the factors. Day and night catches of juvenile whiting (<20 cm) show little difference in the late summer and autumn (Parrish et al. 1964, Bailey 1975, Robb 1981, Ehrich and Gröger 1989, Paper III) which may indicate that diel changes in catchability of this species are minor in this season and hence also the extent of vertical migration and visual avoidance or herding. In this case, the daily average catch provides the minimum variance index of the density near the bottom. In the case of prey species which perform pronounced diel vertical migrations (e.g. clupeids (Blaxter and Parrish 1965)), the density should preferably be estimated at the time of day where the predator feeds on this prey. Dawn and dusk periods are likely to be important feeding periods (Blaxter and Parrish 1965, Hobson 1986, Major 1977) but they are also the times of day where the greatest changes in density in the bottom channel takes place (Blaxter and Parrish 1965, Hjellvik et al. 2002a). Hence the estimate will depend heavily on whether catches were taken before or after sunset, even in the case where only an hour or less passed between the trawl hauls. Density at dawn and dusk is likely to be intermediate between day and night densities, and daily average trawl catch rates seems preferable as an estimate of these intermediate densities. Hence the daily average catch was considered the best achievable estimate of average density of all fish prey in the demersal layer in

this study. As all hauls were standardised with respect to distance (V was constant), the absolute catch rather than catch rate was used.

Density dependent catchability changes

A startled fish will behave differently depending on whether it is alone or in the vicinity of conspecifics (Morgan 1988, Domenici and Batty 1997). Similar differences in behaviour have been seen within the mouth of a trawl, where single gadoids seemed to be more agitated and had a higher probability of escaping the trawl than fish who encountered other gadoids of a similar size (Godø et al. 1999). When other gadoids were present, they would swim together in a school and show limited escape reactions (Fig. 3). Eventually, they would fall back in the trawl and be caught. The probability of catching individual fish in the trawled volume thus increased with the density of fish. This effect depends on the ability of the fish to keep pace with the trawl for some time and hence would not be expected to be present in small fish (Main

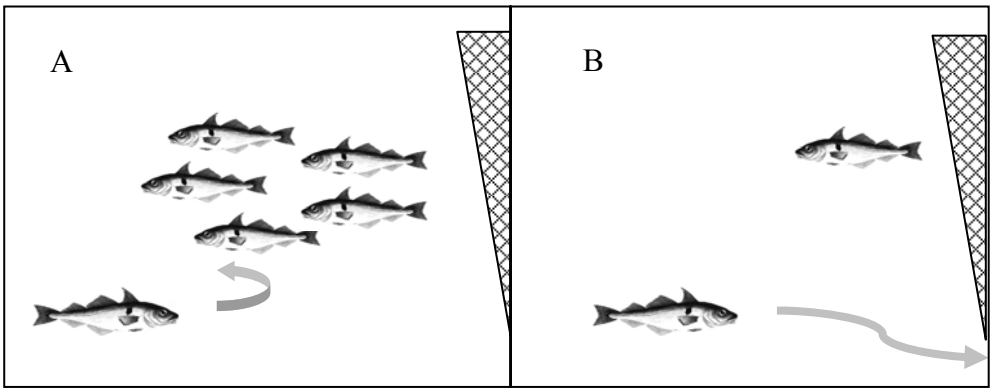

Fig. 3. The behaviour of haddock and cod in the mouth of the trawl. When several similar sized fish are swimming just ahead of the trawl, fish encountering the trawl will join the shoal and eventually fall back into the trawl and be caught (A), whereas a fish encountering few or no other fish in the mouth of the trawl will attempt to escape through the meshes or below or above the trawl (B). Redrawn from Godø et al. (1999).

and Sangster 1981, Hammer 1994). Small gadoids instead press to the bottom when encountering a trawl (Engås and Godø 1989b, Walsh 1991) and catchability of these individuals is unlikely to be affected by shoaling in the mouth of the trawl (Main and Sangster 1981). The catchability of species that are obligate schoolers like clupeids should likewise be independent of density as these rarely occur without conspecifics. In contrast to the positive effect of density of larger gadoids on catchability, juvenile cod have been shown to have a greater vertical distribution and hence lower catchability when density is high (Godø and Wespestad 1993). However, this will affect both trawl catch rates and the density of prey experienced by the predator equally (given that vertical migration by the predator is limited), and hence the trawl should provide an unbiased estimate of both clupeids and juvenile gadoid density in the demersal layer.

Estimation of food intake of fish

Estimates of food intake of fish predators in their natural environment can be obtained either from bioenergetic modelling (Horton 1961, Malyshev 1980, Majkowski and Waiwood 1981, Hansson et al. 1996) or by combining knowledge of stomach contents with estimates of the evacuation rate of these contents (Bajkov 1935, Daan 1973, Jones 1974, Elliot and Persson 1978, Pennington 1985). The former method combines knowledge of growth rates, metabolism and activity and provides an estimate of the amount of energy required to cover these needs. This renders the method well suited for the estimation of consumption over a longer period such as a number of months. However, the food intake over such long time spans provides no knowledge of prey composition and short term food intake. This type of information can,

however, readily be obtained by the combination of average stomach content in the field and evacuation rates for different prey types.

Estimating food intake from stomach contents

Estimating food intake from stomach contents was proposed as early as 1935 by Bajkov (1935) who suggested that the number of prey found in the stomachs should be directly proportional to the number of prey eaten daily, the proportionality factor being equal to the number of days after ingestion a prey could be recognised in the stomach contents. Later experiments have shown that the time taken to evacuate the individual prey items can not generally be assumed to be independent of the number of prey present in the stomach (Elliot and Persson 1978, DosSantos and Jobling 1992, Temming and Andersen 1994)), and so the direct proportionality does not hold. The lack of proportionality has led to the proposition of a large number of alternative methods to estimate food intake from stomach content data (e.g. Elliot and Persson 1978, Pennington 1985, Dos Santos and Jobling 1995, Temming and Mergardt 2002). Unfortunately, the implementation of the majority of these methods has been based on erroneous assumptions on either the statistical distribution of the total stomach contents, the occurrence of individual prey types in the stomach or the evacuation rates of individual prey types (Paper V). These unwarranted assumptions have resulted in substantially biased estimates of food intake, and to avoid this, a new estimate of the intake of individual prey types was suggested (Paper V). The new estimate calculates the average hourly intake of prey species i in wet weight, C_i, from stomach samples taken over a H hour period as (Paper V):

$$C_i = \frac{\rho_i'}{no}\sum_{j=1}^{no}\sqrt{\hat{S}_{i,j}} + \frac{1}{H}\left(\hat{S}_{i,no} - \hat{S}_{i,1}\right)$$

where $\hat{S}_{i,j}$ and $\sqrt{\hat{S}_{i,j}}$ are the average content of *i* in the stomachs in sample *j* in gram and the average square root of the contents, respectively, *no* is the number of samples taken and ρ_i' is the prey species specific evacuation rate corrected for the effect of other food in the stomach. ρ_i' is estimated from the amount of other food occurring together with prey *i* in the stomachs and the specific evacuation rates of both prey *i* and other food (Paper V). The estimated food intake in wet weight is readily transformed into the number of prey eaten by dividing C_i with the wet weight of the individual prey (Paper VI).

A crucial factor when using this or related methods is accurate knowledge of evacuation rates of the specific prey types. These have been estimated in laboratory experiments for a number of prey species (Dos Santos and Jobling 1992, Temming and Andersen 1994, Andersen 1999, 2001). Alternatively, they can be estimated from field data, and indeed this may be the only way to estimate evacuation rates of prey which can not readily be obtained for use in laboratory experiments (Paper IV).

Comparing food intake at differing temperatures

The capacity of the digestive system of fish is generally determined by the evacuation of food from the stomach as is evident from the link between stomach fullness and appetite which is seen in a number of species (Grove et al. 1978, Gill and Hart 1998, Seyhan et al. 1998, Paper II). Evacuation of food and hence maximum food intake of the predator is strongly dependent on temperature, predator size and prey type (Dos Santos and Jobling 1992,

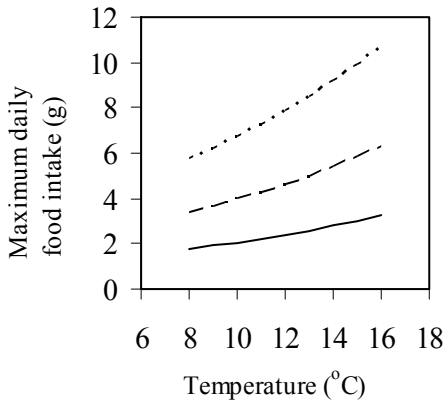

Fig. 4. Maximum daily food intake of whiting of length 20 cm (——), 25 cm (- - -) and 30 cm (····) as a function of temperature. Estimates are calculated by assuming that the maximum sustainable stomach content is 3% of the bodyweight (Calculated as described in Paper VI).

Temming and Andersen 1994, Andersen 1999, 2001)(Fig. 4). A food intake of 6 g/day by a 30 cm fish may thus correspond to full satiation of the digestive system in cold waters but only a fraction of the capacity in warmer waters (Fig. 4). Food intake measures should therefore be corrected for temperature before it is attempted to determine if the predator is physiologically satiated (Arrhenius and Hansson 1994, Essington et al. 2000, Paper VI). This can be done by dividing the amount eaten by the maximum digestive capacity at the given temperature, C_{max}:

$$P_i = \frac{C_i}{C_{\max}}$$

(Paper VI). P_i then provides an estimate of relative satiation which is unaffected by temperature. The procedure obviously requires a measure of the maximum sustainable ingestion rate of the predator. Gadoid stomachs may contain as much as 17% to 19% of the weight of the unfed predator (Temming and Mergardt 2002, Paper II), but the fish are unlikely to be capable of maintaining such high stomach contents over longer time periods and the maximum sustained content is likely to be around 3% bodyweight (Paper VI). To maintain this bodyweight, the predator would have to have an hourly consumption equal to

$$C_{\max} = \rho\sqrt{0.03BW}$$

where ρ is the evacuation rate of the total stomach content at the ambient temperature and *BW* denotes bodyweight of the predator (Pennington 1985, Paper VI). This is an approximation and the estimate could most likely be improved by laboratory experiments. Having estimated the maximum sustainable daily food intake at a given temperature, satiation level can be compared even in the case where the samples were collected at different temperatures.

Food intake and selection

The study of food intake and food selection has evolved from the descriptive studies of Holling (1959b) to complicated deductive models that allow the predator to regulate feeding in response to prey densities, survival probability and physiological state (Mangel and Clark 1986). Generally, the models can be divided into two groups; descriptive models which divide the relationships between food intake and prey density into a number of frequently occurring patterns and deductive models which seek to explain food intake and selection from inherent properties of the prey and predator. In spite of the apparent difference between these groups, several of the models are based on the same fundamental model, the multispecies generalisation of Hollings 'disc' model (Holling 1959a) suggested by Murdoch (1973) and hence the difference often lies in the interpretation of the parameters rather than in the formulation of the model (Murdoch 1973, Stephens and Krebs 1986).

Descriptive models

In 1959, Holling suggested that the response of predators to changes in the density of their food could be divided into three general types of *functional responses* (Fig. 5, Holling 1959b). Predators that show no change in encounter rate and capture efficiency with prey density exhibit a linear increase in consumption with density of their prey, a *type I* response (Fig. 5A). The increase in consumption will continue until a saturation level is reached after which a further increase in prey density has no effect. This response has been found in smaller marine organisms such as *Artemia* and *Daphnia* (Holling 1965). However, most predators will either decrease their search rate or increase the time used to handle prey as food intake increases (Holling 1965, Lipcius and Hines 1986, Mattila and Bonsdorff 1998, Buckel and Stoner 2000, Koski and Johnson 2002). This leads to a decelerating curve that asymptotically approaches a saturation level as prey density is increased (Fig. 5B), a *type II* response. Such a response may also be found in cases where an increase in prey density decreases the vulnerability of the individual prey, e.g. by schooling, herding or common defence mechanisms. A type II response has been found in numerous studies of aquatic predators (e.g. Lipcius and Hines

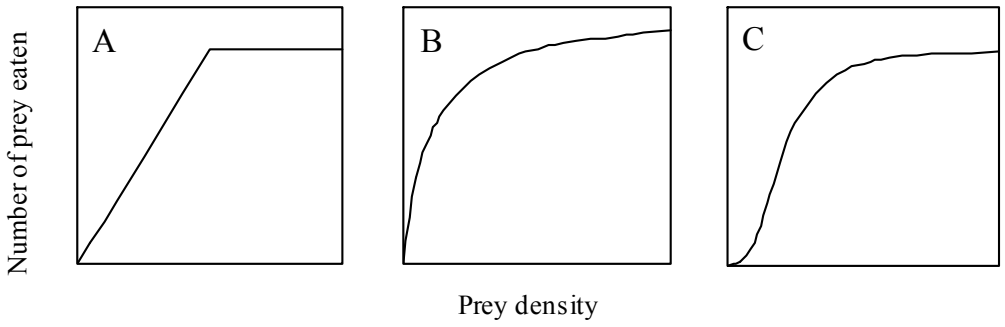

Fig. 5. Functional response types suggested by Holling (1959a). A: Type I, B: Type II and C: Type III. Redrawn from Holling (1959a).

1986, Colton 1987, Buckel and Stoner 2000, Koski and Johnson 2002). It has been deduced theoretically in the form named the 'disc' equation (Holling 1959a):

$$n = \frac{aN}{1 + atN}$$

where n is the number of prey eaten per time unit, N is prey density (prey per area), a is instantaneous rate of prey discovery (area searched per time unit) and t is the time taken to 'handle' prey (time units per prey). 'Handling' may refer to either the time to capture prey (time limited predator) or the time taken to evacuate the prey (digestive capacity limited predator)(Jeschke et al. 2002).

The third functional response, the *type III* response (Fig. 5C), relates to predators whose ability to capture prey increases with increasing density, either due to learning or due to the presence of a limited number of appropriate shelters which render the prey more susceptible to predation as density is increased (Murdoch 1973, Walters and Juanes 1993, Gotceitas and Brown 1993a). Real (1979) proposed a general model to describe type II and III responses:

$$n = \frac{KN^{\beta}}{\chi^{\beta} + N^{\beta}}$$

where K is the saturation level of the predator, χ is the half saturation constant and β is a constant which determines the type of the relationship. β=1 results in a type II relationship whereas β>1 results in a type III response. Increasing β results in increased maximum acceleration of the curve (more pronounced sigmoid shape). Note that it can be rearranged to Hollings 'disc' equation by substituting β=1, a=K/χ and t=1/K.

Murdoch (1973) noted that the type II response appeared to be the most common, and suggested a multispecies extension of this response. The model,

here denoted the *multispecies functional response*, is based on the assumption that a predator limited by the time available to capture and process prey will decrease the time available to feed on one prey as an increasing number of alternative prey is consumed (Fig. 6A). The model describes the number of prey *i* eaten per time unit, n_i, as

$$n_i = \frac{a_i N_i}{1 + \sum_{j=1}^{J} a_j t_j N_j}$$

where subscript *i* and *j* denotes prey type and *J* is the number of prey types included in the diet. This model is also referred to as the *multispecies version of Hollings disc equation* (Chesson 1989, Christensen et al. 2000). It has a number of inherent properties. First of all, the response of a predator to a given combination of prey densities is given directly by the single prey response of the predator to the individual prey (Colton 1987). Secondly, the ratio between the number of prey *i* eaten and the number of prey *j* eaten is directly proportional to their relative densities as

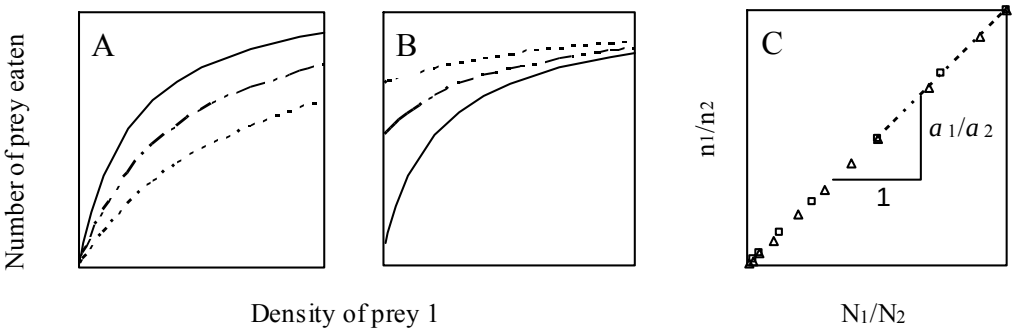

Fig. 6. Number of prey eaten as a function of density of prey 1. Number of prey 1 eaten (A), total number of prey eaten (B) and the ratio between the number of prey 1 and 2 eaten as a function of the ratio between the density of prey 1 and 2 (C). Density of prey 2 1% (———) 10% (- - - and △) and 20% (···· and □) of maximum prey 1 density.

$$\frac{n_i}{n_j} = \frac{a_i}{a_j}\frac{N_i}{N_j}$$

(Fig. 6C). This is in contrast with another food selection model suggested by Murdoch (1969), the *switching model*, in which the relationship is accelerating rather than proportional (i.e. a_i/a_j is an increasing function of N_i/N_j). This model has been used to describe predators which develop a search image of the most abundant prey (Elton and Greenwood 1970), decrease handling time for the most familiar prey (Murdoch 1969) or forage on two spatially separate prey types (Murdoch et al. 1975). However, a number of investigations have found a decelerating rather than accelerating relationship between n_i/n_j and N_i/N_j. This has been denoted *anti switching* (Chesson 1978), *counter switching* (Visser 1981) or *negative switching* (Chesson 1984) and shall henceforth be named by the latter of these names. Several biological explanations for this phenomenon have been suggested (Visser 1981, Kean-Howie et al. 1988, Chesson 1984). Kean-Howie et al. (1988) observed sticklebacks feeding on fish larvae and small zooplankton and suggested that negative switching could arise when a large number of the most abundant prey confused the search image of the predator and caused the fish to eat less of the more abundant species. A similar mechanism was suggested by Visser (1981) who suggested that the least abundant prey became the most conspicuous as it occurred on a background of numerous other prey of a different type, which would lead a predator feeding according to optimal foraging theory (see the section on deductive food selection models) to exhibit negative switching. Visser (1982) also suggested that the phenomenon could occur if the predator attempted to maintain a diet with a balanced composition of micronutrients. Abrams and Matsuda (1993) suggested that negative switching could be generated if a prey attempted to avoid the predator more actively when the rate of predation was high and

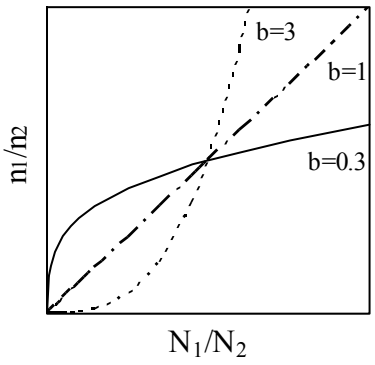

Fig. 7. The number of prey i eaten relative to that of prey j as a function of the relative density of prey i to j. Negative switching (b=0.3), no switching (b=1) and switching (b=3).

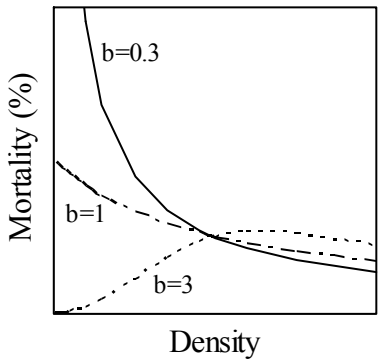

Fig. 8. The effect of switching on the relationship between the mortality and density of prey i given that the density of prey j and total intake is kept constant. b=0.3: negative switching, b=1 no switching and b=3: positive switching.

lastly, Chesson (1984) found that negative switching could occur when the mean preference was estimated as an average of several individuals with different preferences.

Both switching and negative switching can be described by the general switching model (Elton and Greenwood 1970, Visser 1981, Kean-Howie et al 1988, Paper VII):

$$\frac{n_i}{n_j} = \alpha_{ij}\left(\frac{N_i}{N_j}\right)^b$$

where α_{ij} is the preference for prey *i* relative to prey *j* when $N_i=N_j$ and *b* is a constant. If $b>1$, relative preference for a prey increases with density (switching or positive switching), $b<1$ describes the case where relative preference decreases with density (negative switching) and at $b=1$, no switching takes place (Fig. 7).

The presence or absence of switching or negative switching has profound effects on the ability of the predator to stabilize prey populations as is readily apparent by assuming that the predator eats a fixed amount, n_Σ, of prey daily and experiences a varying density of prey *i* while that of *j* is kept constant. In this case the general switching model can be rearranged to

$$\frac{n_i}{N_i} = \frac{n_\Sigma \alpha_{ij} N_i^{b-1} N_j^{-b}}{1 + \alpha_{ij} N_i^b N_j^{-b}}$$

and hence the mortality rate of prey *i* is solely a function of the density of *i* when n_Σ, α_{ij}, b and N_j are kept constant. To stabilize a prey population, the predator must impose an increasing mortality as density is increased (Murdoch 1994, Pelletier 2000) and in a homogenously mixed population, this occurs only when the predator exhibits positive switching and even then it is limited to prey densities below a certain level (Fig. 8) (Murdoch and Oaten 1975).

Deductive models

The idea of discovering the inherent mechanism by which the predator chooses its prey has intrigued ecologists for decades. Among the historically most important theories in the aquatic context are the theory of fitness optimization and the theory of the apparent size of prey. The latter theory describes size selection as the result of the limited ability of fish to determine the size of their prey (O'Brien et al. 1976, Eggers 1977, Butler and Bence 1984, Li et al. 1985). Planktivorous fish generally have a poor ability to determine absolute size and may rely on the angle the prey occupies in the visual field and large prey will hence be attacked from a larger distance than small (O'Brien et al. 1976). This model was developed to describe food selection by fish feeding on zooplankton and is unlikely to apply to piscivores, which are not limited by visual acuity (Breck 1993). In contrast, the theory of fitness optimization, should theoretically describe food selection by fish and has been studied in numerous experiments (e.g. Werner and Hall 1974, Mittelbach 1983, Bannon and Ringler 1986, Hart and Gill 1993). When the theory was introduced, most authors equated optimization of fitness to

ingesting the greatest possible amount of energy in the least possible time (Emlen 1966, MacArthur and Pianka 1966). A forager should rank prey according to the amount of energy they contain divided by the time required to capture and handle them (Emlen 1966, MacArthur and Pianka 1966, Stephens and Krebs 1986). Only the highest ranked prey should be included in the diet when this prey was abundant whereas lower ranked prey would be ingested when higher ranked prey were scarce. This version of fitness optimization, *optimal foraging theory* (Stephens and Krebs 1986), can be described by the general switching model (Page 31) if the predator is forced by low prey density to feed on several prey types and encounter rate is proportional to or a power function of density (Paper VII). If encounter rate is proportional to density, the intake of the most preferred prey type should furthermore be well described by a single species type II functional response, whereas that of less preferred prey should follow a type II response only in the absence of saturation with the more preferred prey. Hence optimal foraging should result in tight single species functional responses to one or more prey, but a poor single species functional response to all but one prey in the cases where the predator is able to achieve saturation by feeding on the preferred prey type only. If the density of the preferred prey is high enough to saturate the predator, all other prey should be ignored.

An alternative version of the fitness optimization theory is the *unifying foraging theory* (UFT) proposed by Mangel and Clark (1986). They assume that the predator will choose the strategy that maximizes its long term fitness measured as e.g. reproductive output. The chosen strategy depends on both profitability of the prey, the current nutritional state of the predator and the mortality risk taken by the predator when feeding (Mangel and Clark 1986, Hart and Gill 1993, Alonzo and Mangel 2001). The flexibility of UFT makes it

appropriate for a wide range of predators (Mangel and Clark 1986). However, to test the model in detail would require substantial knowledge of mortality rates, predator bioenergetics and numerous other factors. Such knowledge is difficult if not impossible to obtain in a field investigation. Nevertheless, one of the predictions of the model can be tested as UFT is the only theory which predicts that predator diet can be affected by the nutritional state of the predator at any level other than through digestive satiation. Hence a correlation between the nutritional state of the predator and food selection may indicate that prey selection is state dependent and hence a more complicated process than assumed in other models.

Selection between temporally segregated prey

Inherent in any food selection model is the theory of exclusiveness of choices: the predator cannot reach its saturation level of two prey at the same time as feeding on one prey invariably decreases the time available to capture and digest other prey. However, this constraint does not necessarily describe the feeding situation of a piscivore with a broad diet. The diverse prey types fed on by e.g. gadoids (Jones 1954, Adlerstein and Welleman 2000) are not equally available at all times of day (Blaxter and Parrish 1965, Hobson 1986, Pitcher and Turner 1986) and as a result of this some prey types are eaten only during very limited periods of the diel cycle (Paper III, Paper VI, Fig. 9). Whiting in particular appear to feed on benthic prey during the night whereas free swimming prey such as fish and krill are eaten during the day (Paper III, Paper VI). Feeding on fish prey appear to be most intense around dawn and dusk, perhaps due to the increased visibility or the decreased vigilance of prey to predators at low light levels (Blaxter and Parrish 1965, Hobson 1986, Pitcher and Turner 1986, Paper VI). As both clupeids and gadoids are eaten during this

period, chasing one prey must limit the time available to chase other prey and the choice between fish prey would appear to be exclusive. In contrast to this, the intake of benthic prey may be independent of that of fish prey if the benthic prey eaten during the night is digested to a state where it does not inhibit feeding on fish prey at dawn. A significant proportion of the whiting caught indeed appeared to be reluctant to feed and their intake of fish may have been inhibited by digestive processing rate (Paper II). However, though prey eaten in the last part of the night may inhibit feeding activity at dawn, this is not necessarily the case for prey eaten just after dusk, and hence neither complete exclusiveness nor complete independence of choices exists. Describing food selection in this environment is likely to be complicated, in particular if the predator alters its preferences when the stomach contains food. A number of fish species reduce meal size when the stomach is partially filled and hence in a natural environment would most likely prefer smaller prey (Grove et al. 1978, Hart and Gill 1993, Sims et al. 1996). This may shift the preference of the

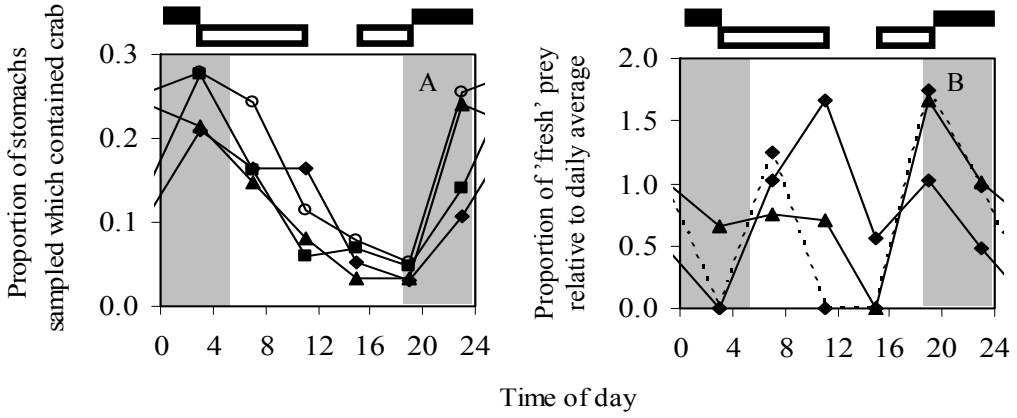

Fig. 9. Diel pattern in food intake of whiting. The proportion of stomachs which contained crab (A) and the relative occurrence of fresh clupeids in the stomachs (B) as a function of time of day. A: each symbol indicate data from predators of length 25 to 30 cm from one location. B: sprat (▲) and herring (◆). Bars above plots indicate main feeding periods on clupeids (white) and crabs (black). Redrawn from Paper III (A) and VI (B).

predator from larger to smaller prey items and thus severely complicate the estimation of preferences. Though such effects occur in some species, whiting in the wild do not appear to decrease meal size as stomach content is increased (Paper II) and hence no inherent effect of stomach fullness on prey preferences of this predator exists. The preference for a particular daytime prey relative to another daytime prey should therefore be unaffected by night time feeding and relative preferences between daytime prey can be estimated without complications. The estimation of a multispecies functional response is, however, complicated by temporal segregation. The saturation level of daytime prey could theoretically be reduced by ingestion of other prey during the night. If this is the case, the sum of fish intake and the intake of other food should equal the maximum food intake rate. Otherwise, the multispecies functional response should provide a description of the ingestion of fish prey by whiting, and in particular, the prediction of constant preference for one prey relative to another should still apply.

Estimation of food selection in a marine environment

Estimation of parameters in any food selection model requires contemporary knowledge of food intake and prey density. This presents a problem as the absolute density of prey is rarely known in a marine environment. However, a number of parameters in the food selection models can be estimated even in the absence of absolute density estimates if an index of prey density is available. Trawl catch can be considered such an index if catchability can be assumed constant for each prey type as then $T = qN$. Inserting $N = q^{-1}T$ and $P = C/C_{max} = n/n_{max}$ in the general functional response

suggested by Real (1979), the relationship between relative satiation, P, and trawl catch, T, becomes

$$P = \frac{K'T^{\beta}}{(q\chi)^{\beta} + T^{\beta}} = \frac{K'T^{\beta}}{(q\chi)^{\beta} + T^{\beta}}$$

where $K' = K/n_{max}$ and n_{max} is the maximum number of prey that can be eaten (Paper VI). Hence the saturation level of the relative satiation, K', can be estimated directly by comparing P and T whereas χ can only be estimated as the trawl catch corresponding to half saturation, $q\chi$. Inserting the same relationship between density and trawl catch in the multispecies functional response, the model becomes

$$P_i = \frac{a'_i T_i}{1 + \sum_{m=1}^{m=M} a'_m t'_m T_m}$$

where $a'_i = a_i q_i^{-1} n_{max}^{-1}$ and $t'_i = t_i n_{max}$. The saturation level of the individual prey (t_i^{-1}) is again determined directly whereas a_i (and hence prey preference) can only be estimated as the product $a_i q_i^{-1}$. Similarly, inserting $N_i = q_i^{-1} T_i$ in the general switching model, the relationship becomes

$$\frac{n_i}{n_j} = \alpha_{ij} \frac{q_i^{-1}}{q_j^{-1}} \left(\frac{T_i}{T_j} \right)^b$$

or on a logarithmic scale

$$\log\left(\frac{n_i}{n_j} \right) = \log\left(\alpha_{ij} \frac{q_i^{-1}}{q_j^{-1}} \right) + b \log\left(\frac{T_i}{T_j} \right)$$

The general switching model thus requires the relationship between the relative amount of prey i in the diet and the relative amount in the trawl of prey i to be a straight line with slope equal to b when observations are plotted on a log-log scale. As the number of prey i ingested is always examined relative to prey j,

an increase of the total amount that can be eaten by e.g. 50% will affect both and cancels out of the equation. Whereas *b* can be estimated directly, the relative preference for a prey can only be estimated as the combined effect of preference and relative catchability. Note that when food intake is estimated from stomach content, it is a historical estimate based on food eaten as early as several days prior to the stomach sampling (Paper II, Paper VI). If the predators migrate, they may have encountered prey densities quite different from the current situation. This will add to the variation around the relationship between local prey density and food intake.

Food selection by North Sea whiting

The data used in this study originated from intensive sampling of whiting at five locations in the North Sea and is described in detail in Papers II to VII. Briefly, stomachs were sampled from whiting caught by trawling every four hours for 2 or 3 consecutive days. The locations sampled differed in depth, temperature and prey density (Paper VI).

There did not appear to be mutual exclusiveness of fish and other prey in the diet of the whiting analysed (Fig. 10). This may have been caused by the general lack of digestive satiation (Paper VI, Fig. 10). Nevertheless, intake of both other food and fish prey seemed to reach an asymptote at around 25 % of maximum intake (Paper VI). The saturation of fish intake occurred at high

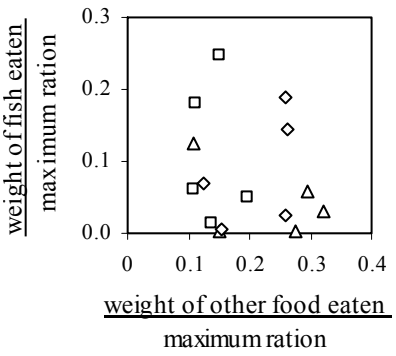

Fig. 10. The weight of fish prey eaten as a function of the weight of other prey eaten, both relative to the maximum ration. Whiting of length 20 to 25 cm (△), 25 to 30 cm (◇) and 30 to 35 cm (□). Redrawn from Paper VI.

fish prey densities whereas that of other food occurred at temperatures above 10 ^{o}C. The exact reason for the saturation of the intake of other food could not be determined but it may have been caused by either changes in search rates, increased densities or a combination of the two. Whatever the reason, the intake of other food appeared to be considerable. This was not the case, however, if sampling was restricted to daylight as the estimation of the intake of e.g. crabs decreased by 30 to 50% if night time samples were excluded (Paper V). This may be part of the reason for the general conception of whiting as a major piscivore, as most previous investigations of food composition have been based on stomachs collected mainly during daylight (Jones 1954, Gordon 1977, Patterson 1985, ICES 1991, ICES 1996). However, there are seasonal changes in the diet of whiting (Jones 1954, Patterson 1985, Hislop et al. 1991), and the result here may only imply that whiting feed on non fish food to a large extent in the early autumn.

The single species functional response to herring was well described by a slightly sigmoid curve (Paper VI, Fig. 11A). The fit of the response to sprat was somewhat poorer (Fig. 11B) but as the data point lying below the curve at

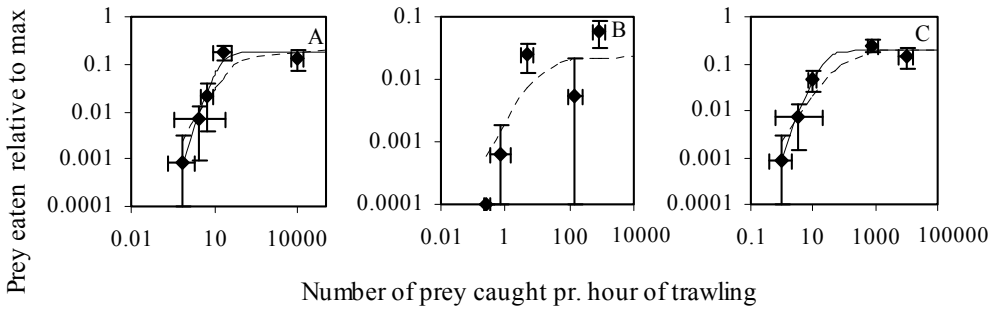

Fig. 11. Functional response to herring (A), sprat (B) and total clupeid density (C). Food intake is measured relative to the maximum intake to make observ ations comparable in spite of differences in temperature between locations. Bars indicate 95% confidence limits of the estimates. - - -: Type II response. ——: Type III response. Redrawn from Paper VI.

the second highest sprat density corresponded to the location with the highest herring density, the low intake of sprat at this location did not decrease total clupeid intake (Fig. 11C). This may indicate that sprat is a less profitable prey than herring and that the predator was foraging according to optimal foraging theory. However, contrary to this theory, sprat was actually the preferred prey at one location (Paper VII). The response to juvenile gadoids was less tight than the response to clupeids (not all confidence limits include the fitted line in Fig. 12B) and the deviations from a smooth curve could not be linked to low availability of herring or clupeids in total, as the second highest intake of gadoids was found at the highest density of herring (Fig. 12). Hence, there appeared to be some support for optimality in the foraging behaviour in the close fit of a single species functional response to the intake of herring. However, the predator fed on other fish prey as well as herring even at high herring densities, and this is in direct opposition to optimal foraging theory.

The intake of all fish prey saturated at a level well below digestive capacity (Paper VI, Fig. 11, Fig. 12). This could theoretically have been caused

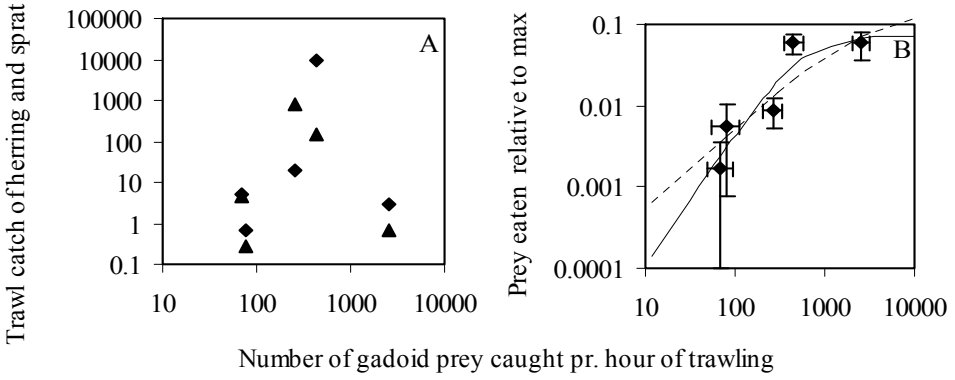

Fig. 12. The catch of clupeids as a function of the catch of juvenile gadoids (A) and the functional response of whiting (25 to 30 cm) to juvenile gadoids (B). A: catch of herring (◆) and sprat (▲). B: bars indicate 95% confidence limits of the estimate. - - -: Type II response. ——: Type III response. Redrawn from paper VI.

by a handling time saturation being reached before a digestive satiation (Jeschke et al. 2002). However, in the present study, the implied time to capture and handle prey would be in excess of 10 days (Paper VI), and as other piscivorous fish are able to capture and ingest prey within a matter of minutes (Major 1978, Gotceitas and Brown 1993), it seems unlikely that handling time limitation was the reason for the low saturation level. Lack of digestive saturation at high prey densities has also been found in a study of largemouth bass (*Micropterus salmoides*), which consumed only 50% of maximum daily ration in their natural environment though prey density was very high (Essington et al. 2000), and the phenomenon could be general in piscivorous fish.

The multispecies functional response provided a poor fit to the observed food intake (Paper VI). The problem was evident when the amount ingested of one prey relative to that of another was plotted (Paper VII, Fig. 13). The

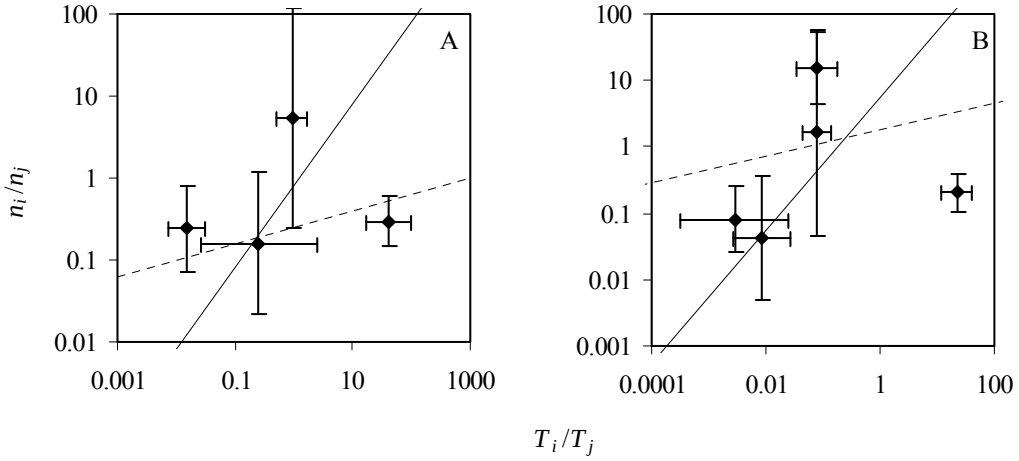

Fig. 13. The amount of prey *i* eaten relative to the amount of prey *j* eaten by whiting (25 to 30 cm) as a function of the relative number caught of the two species. Sprat relative to herring (A) and herring relative to whiting (B). Bars indicate 95% confidence limits of the estimates. Solid line indicates no switching (b=1), hatched line indicates pronounced negative switching (b=0.2). b=0.2 was the highest value of b that produced estimates within the 95% confidence limits of the observed values of sprat relative to herring. Redrawn from Paper VII.

multispecies functional response requires this relationship to be proportional and hence linear with a slope of one in a log-log plot (the solid line in Fig. 13). This model clearly provides a poor description of the observations. Attempting to describe the observed selection by the general switching model, it was clear that the predators exhibited an extreme case of negative switching as *b* must be around 0.2 to describe the preference for sprat relative to herring (Paper VII, the hatched line in Fig. 13). A similarly low value of *b* is required to describe the selection between herring and whiting, though this relationship is rather poorly described by the general switching model. The substantial degree of negative switching supports the findings of a preliminary study of food selection of cod and whiting (Rindorf et al. 1998). The authors detected negative switching in both cod and whiting using the general switching model, and the estimates of *b* ranged from 0.14 to 0.34. However, the general switching model did not provide a better fit to data than the simple single species functional responses in this study.

Looking more closely at the single species functional responses, the residual error appeared to be correlated to predator density, as sprat was eaten to a greater extent at high predator densities where less juvenile whiting were consumed (Fig. 15). This correlation could suggest that predators in groups were more efficient at catching schooling prey as has been shown to be the case for jacks (*Caranx ignobilis*)(Major 1978). Juvenile gadoid prey may seek refuge from predation to a greater extent at high predator densities (Walters and Juanes 1993, Gotceitas and Brown 1993a, Gotceitas et al. 1995) and therefore become less available at high predator densities. Alternatively, individual predators may interfere when pursuing gadoids and hence decrease the per capita intake as predator density is increased (Beddington 1975, Arditi and Akçakaya 1990). Both effects should lead to an apparent increase in

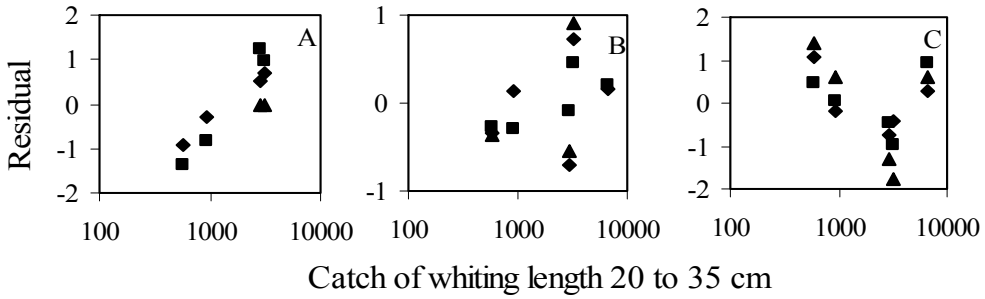

Fig. 15. The residual of the single species functional response (ln(observed intake)-ln(predicted intake)) as a function of predator density. Sprat (A), herring (B) and gadoids (C). Functional response of sprat was estimated as type II, of herring and gadoids as type III. The highest catch of predators was taken at the location where sprat was virtually absent. Rindorf, unpublished results. Based on functional response, food intake and predator densities given in Paper VI.

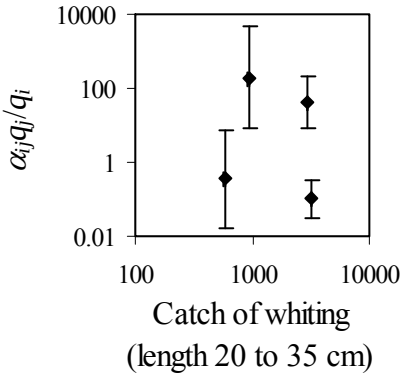

Fig. 14. Preference/catchability of sprat relative to whiting of whiting 30 to 35 cm long as a function of catch of predators. Bars indicate 95% confidence limits. Confidence limits of catch of predators were too narrow to be seen in the plot. Rindorf, unpublished results. Based on consumption and catch estimates given in Papers VI and VII.

preference for sprat compared to whiting as predator density increased. However, no such pattern could be detected (Fig. 14), and hence the correlation between single species functional response residuals and predator density may be the result of random effects in a small data set.

There was some indication that predator condition could influence preference (Paper VII, Fig. 16). It seemed that whiting preferred herring more strongly relative to both sprat and juvenile whiting when well fed. In contrast to this, no trend in the preference for sprat relative to whiting as a function of condition could be detected (Rindorf, unpublished results). A correlation between condition and total food intake has previously been

demonstrated in Arctic charr (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*), where food intake decreased as condition increased (Jobling and Miglavs 1993, Simpson et al. 1996). Cod grow optimally on a diet consisting almost solely of herring (Jobling et al. 1991), and this prey may be equally profitable for whiting. If this is the case, whiting may prefer herring to achieve optimal growth when condition is high but prefer sprat when it is necessary to regain condition after having lost weight. Sprat is a lipid rich fish with a much higher energy content than herring (herring<14 cm, Pedersen and Hislop 2001) and a diet rich in fat may optimise the rebuilding of depleted reserves though it does not optimise somatic growth (Lie et al. 1988, Jobling et al. 1991). Alternatively, the correlation between condition and preference may be a mere chance result as the number of points in Fig. 16 is obviously low. If this is the case, the general switching model is the only model examined here which can explain the lack of constant preference which would be expected from an

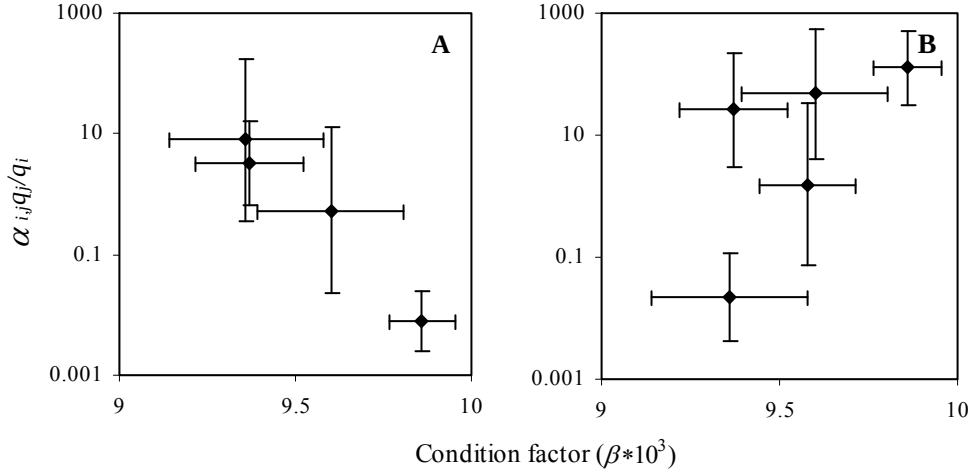

Fig. 16. Preference for prey i relative to prey j of whiting of length 30 to 35 cm as a function of average condition of predators caught at the location. Sprat relative to herring (A) and herring relative to whiting (B). Increased values of preference/catchability indicates increased preference/catchability for the former prey. Bars indicate 95% confidence limits of the estimates. Redrawn from Paper VII.

optimally foraging (energy maximising) predator or a predator foraging according to the multispecies functional response.

Negative switching is not unknown in the literature, though the authors often do not recognise the response and simply note that no (positive) switching occurred. Three spined sticklebacks (*Gasterosteus aculeatus*) exhibited negative switching between several prey types, and the estimate of *b* was 0.66 in the study where this figure was calculated (Visser 1982, Kean-Howie et al. 1988). Similar results were found in a preliminary study of switching in cod and whiting in the North Sea (Rindorf et al. 1998). Buckel and Stoner (2000) looked for positive switching in bluefish, *Pomatomus saltatrix*, and concluded that no switching could be detected. However, it is evident from their Fig. 3 that the fish in fact exhibited negative switching, and reading values from this figure points to a value of *b* around 0.6. Similarly, Gotceitas and Brown (1993b) examined the protective effect of *Calanus* on cod larvae exposed to predation from three spined sticklebacks. Though they did not emphasise results on prey selection, reading values from their Fig. 4 results in an estimate of *b* around 0.4. Thus, though the number of investigations which examine negative switching directly is low, it may occur more generally than this number would suggest.

Biological explanations for negative switching and lack of digestive satiation

The observed negative switching and lack of satiation may be caused by a number of factors. First of all, the predators may attempt to maintain a balanced diet with respect to micronutrients as suggested by Visser (1982). However, gadoids in captivity grow at high rates when given diets consisting

of an even higher percentage fish than the 63% which was the maximum proportion of fish in the diet found in this study (Jobling et al. 1991, Fig. 3 in Paper VI). Further, it is unlikely that a predator in a poor condition would be growing at a high rate, and to this predator the highest priority is likely to be ingesting whatever food it may achieve at a limited cost. This theory therefore provides no explanation for the apparent preference for sprat relative to herring when condition is low. It seems unlikely that the predator became confused by the most abundant prey and hence exhibited negative switching by forming a search image corresponding to the least abundant prey (Visser 1981, Kean-Howie et al. 1988) as herring and sprat are quite similar in appearance. It also seems unlikely that negative switching was caused by changes in prey behaviour in response to increased predation mortality as suggested by Abrams and Matsuda (1993), as the distance to the non-switching line was greatest at the location with the lowest predator density (Paper VII).

A potential source of error in the analyses is the ability of the trawl to provide an unbiased index of the amount of prey available to the predators. A severe increase in catchability of prey fish as their density was increased may result in negative switching. However, the increase would have to be large enough to result in an increase in herring catches by more than 9000 fish (more than 400 times) at a very slight increase in density as herring intake levelled of at a trawl catch of around 20 herring in the present study (Fig. 11). Such an increase can hardly be explained by the mechanisms reported to lead to density dependent changes in catchability in other species (Godø and Wespestad 1993, Godø et al. 1999). The degree of negative switching is furthermore too large to be explained by the aggregation of prey into large groups and the resulting decrease in the visibility of the individual (Paper VII).

The trawl hauls taken in the present study covered a distance of 3.5 nautical miles (Paper II). This corresponds to a travelling time of 3.5 and 2 hours of a predator of length 20 to 35 cm, respectively, swimming at 2.5 body lengths per second caught in one end of the trawl track to reach prey caught in the other end of the trawl track (Hammer 1994). This travelling time corresponds to directional swimming, e.g. the predator must know where to locate the prey. If the behaviour of the prey was unpredictable, the predator would have to search in all directions and travelling time would increase. Thus, if the predator was unable to predict the distribution of prey through e.g. past experience or other clues, it is unlikely that all prey was available to all predators within a reasonable amount of time. This may explain why full satiation was not reached even at very high prey densities as some predators may have been unable to locate the areas of high prey density. The underlying assumption of this is that predators do not aggregate over larger areas in response to prey density and this is in accordance with the lack of aggregative response described in Paper VI and with results for cod preying on capelin (*Mallotus villosus*) and bluefish feeding on anchovies and sandeel (Safina and Burger 1989, Rose and Leggett 1990, Horne and Schneider 1994). As the intake of sprat is decreased at high herring densities, sprat and herring would have to be located in approximately the same area if the result was caused by lack of overlap between predators and prey. In contrast, juvenile gadoids must have been located in adjacent areas as the intake of gadoids should otherwise have decreased at high clupeid densities. Trawl catches of all species were highly consistent within a given time of day and location (Rindorf, unpublished results) and similar consistency has been found in other experiments (Hjellvik et al. 2002b). However, even though the trawl most likely provides a consistent index of the prey abundance, the prey may have been patchily distributed

within the trawl track and this may be the explanation for the lack of digestive satiation of the predators.

Chesson (1984) found that negative switching would be the most likely population result if the preferences differed between individual fish. Such individual preferences have been observed in Atlantic cod, where some individuals readily fed on live fish whereas others did not (Gotceitas et al. 1995). This effect would lead to a saturation level below the physiological maximum as was observed here. Although the analyses performed in this study were unable to detect a tendency for predators to specialise on either fish or invertebrates, the data material did not allow an investigation of whether individual predators specialised on different species of fish. If this was the case, it would lead to lack of exclusiveness of prey choice as herring specialists would continue to feed on herring regardless of whether whiting specialists were saturated or not. Hence negative switching and lack of satiation may be the result of individual differences in preferences, the limited ability of the predator to locate prey at a distance or any combination of the two. Which of these is the dominant mechanism on the local scale does not, however, alter the implications of negative switching for whiting and its prey.

Food selection and ecosystem stability

Several authors have suggested either the type III functional response or positive switching to be a prerequisite of predation induced stability in the absence of an aggregative response (Holling 1959b, Murdoch and Oaten 1975). However, this is true only in a homogenously mixed population, and spatial heterogeneity may induce stability even in models which are unstable in a homogeneous environment (DeAngelis and Waterhouse 1987, McCauley et al.

1996, van Baalen and Sabelis 1999). Thus even though both negative switching and the lack of an aggregative response of the predators will decrease prey mortality rate as local density is increased (Paper VI), this will not necessarily lead to instability if the system is heterogeneous. If a decrease in total density of a prey population leads to decreased density throughout the area, the effect of negative switching will indeed be destabilising. However, clupeids are obligate schoolers and may maintain a lower school size below which schools will join on encounter (Pitcher et al. 1996). This effect would lead to a decrease in the number of schools when density is low (Petitgas and Levenez 1996, Bonabeau et al. 1999). Though individual schools also tend to get smaller at low densities (Petitgas and Levenez 1996), the decrease in the number of schools decreases the exposure to predators which do not show an aggregative response (Paper VI). Further, the proportion of the prey which are gathered in large schools seems to increase slightly as density is decreased (Petitgas and Levenez 1996). Hence a large population with numerous schools may suffer a higher mortality from whiting predation than a small population comprised of a few schools as few schools will both encounter fewer predators and have larger average size. This may save prey populations from complete extinction and add to the stability of the ecosystem. Furthermore, in combination with the apparent lack of physiological satiation, it disrupts the simple relationship between prey density and predator growth and reproduction expected in a homogeneously mixed population (e.g. DeAngelis and Waterhouse 1987, McCauley et al. 1996). Increasing the herring population to a high level at all locations does not necessarily lead to optimal growth as the predators appear to be saturated at a level well below the food intake required to maximise growth of gadoids in captivity (3-4% body weight per day for cod at a temperature of 11 to 14 ^{o}C, Jones and Hislop 1978). Hence ‘bottom up effects’ (Worm and

Myers 2003) are likely to be difficult to detect in such a system, though they have been demonstrated in cod specialising on capelin (Yaragina and Marshall 2001) and at lower trophic levels (Aebischer et al. 1990).

Conclusions

This study has shown that it is indeed possible to estimate the functional response of fish predators to fish prey in their natural environment by combining trawl estimates of density with consumption estimates based on stomach contents. The lack of temporal overlap between prey types invalidated the use of a number of food selection models as the assumptions of the models were not met, e.g. ingestion of different prey types were not mutually exclusive in the traditional sense. The prediction of total consumption of whiting at a range of differing prey densities would require a new model to be developed which can deal with temporally segregated prey and satiation effects.

The single species functional response provided a good description of the intake of herring and the total intake of clupeids. However, the relative contribution of sprat and herring to the diet was not proportional to their relative density in the surroundings as sprat was only ingested in small numbers unless there was a lack of satiation with herring. Intake of sprat may be enhanced at high predator densities, perhaps due to the increased ability of shoaling predators to locate and capture schooling prey (Major 1978, Pitcher et al. 1982). In contrast to this, the intake of whiting appeared to decrease with predator abundance when clupeid prey was abundant but was otherwise unaffected by clupeid intake.

The model used in most descriptions of predator-prey interactions, the multispecies functional response, provided a poor description of food intake of

whiting and should be used with caution. In contrast, the selection between herring and sprat could be described by the negative switching model. The causes of this phenomenon were most likely either the patchiness of prey or the difference between the preferences of individual predators. However, both predator condition and predator local abundance may have an effect on food selection. Schooling prey and prey which tend to aggregate in fewer patches as their density decreases, may suffer higher mortality at high density if lower density operates through first eliminating low density patches and then eliminating rather than diminishing larger patches. Hence the effect of prey density on the patchiness of prey as well as the aggregative response of the predators are of crucial importance when population effects of negative switching are examined and both factors should be examined further in the future.

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Paper I

Analyses of length and age distributions using continuation-ratio logits

A. Rindorf and P. Lewy

Canadian Journal of Fisheries and Aquatic Science, 2001, **58**, 1141-1152.

Abstract

Sampling of length and age distributions of catches is important for the assessment of commercially fished stocks. This paper presents a new method for statistical analyses and comparisons of length and age distributions based on generalised linear models of continuation-ratio logits. The method allows statistical testing of the effects of both continuous and discrete variables. Further, by utilising the smoothness of length and age distributions as a function of length, the method provides more accurate estimates of these distributions than traditional methods. The observations are assumed to be multinomially distributed, but cases in which the variance exceeds that of this distribution may also be analysed. The implementation of the method in existing statistical analysis software is straightforward and is demonstrated using length and age distributions of the lesser sandeel, *Ammodytes marinus*.

Paper II

The effect of stomach fullness on food intake of whiting in the North Sea

A. Rindorf

Journal of Fish Biology 2002, **61**, 579-593

Abstract

The probability of a North Sea whiting *Merlangius merlangus* stomach containing fresh food was depressed when partially digested food was already present in the stomach. The lowered probability was detected even at levels where the fish was physiologically able to ingest an average meal. The feeding probability of c. 15% of the fish caught was predicted to be severely decreased at the level of partially digested food found in the stomachs. No effect of stomach fullness on meal size was found, indicating that the saturation is affecting search activity rather than prey or meal size selection. The diurnal pattern in food intake varied between the five sampling locations, presumably as a result of differences in prey availability.

Paper III

Diel feeding pattern of whiting in the North Sea

A. Rindorf

Marine Ecology Progress Series, 2003, **249**, 265-276

Abstract

Though numerous studies have analysed the feeding periodicity of North Sea gadoids, no general diel pattern has been found. The lack of agreement between studies may be related to differences in prey composition and behaviour, but it has not been attempted to link the diel intake pattern directly to intake of individual prey. This study presents an analysis of the round the clock occurrence of several prey types in the stomachs of whiting *Merlangius merlangus*, a major predator on fish and crustaceans in the North Sea. Generalised linear models were used to determine if the occurrence of different prey varied significantly with time of day and whether this diel pattern differed between locations and predator size groups. The results show that the occurrence of bottom dwelling prey increased significantly during the night at 4 of 5 locations. In contrast, free swimming prey and prey migrating towards the demersal layer during the day were eaten mainly in the daylight hours. No diel pattern in the presence of larger fish prey could be found, presumably due to their longer digestion time. A general diel pattern in catch rates of the predator could not be detected and the analyses did not appear to be biased by vertical migration of the predator. The results have important implications for

the understanding of prey selection by wild predators, as this is, in effect, a choice between temporally co-occurring prey.

Paper IV

Estimation of evacuation rates in the field

A. Rindorf

Journal of Fish Biology, 2004, ***65***, 262-281

Abstract

Two methods are presented to calculate evacuation rates based on observed diel changes in occurrence and mean mass of prey in predator stomachs. The methods do not require predators to exhibit prolonged non-feeding periods, but the ingestion of each particular prey type must be restricted to certain diel periods. Data from >7500 whiting *Merlangius merlangus* collected at five locations in the North Sea were used to demonstrate the methods. The evacuation rates estimated from field data were similar to laboratory results, though a tendency for estimates to exceed literature values slightly was noted. Bias was introduced if a large proportion of the prey was evacuated completely in the interval between subsequent samples and if significant amounts of other food were present in the stomach together with the prey in question. The methods can be used to supplement laboratory estimates of evacuation rates or provide first estimates for species that are not easily maintained in the laboratory.

Paper V

Bias in estimating food consumption of fish by stomach-content analysis

A. Rindorf and P. Lewy

Canadian Journal of Fisheries and Aquatic Sciences, 2004, **61**, 2487-2498

Abstract

This study presents an analysis of the bias introduced by using simplified methods to calculate food intake of fish from stomach contents. Three sources of bias were considered: (1) the effect of estimating consumption based on a limited number of stomach samples, (2) the effect of using average contents derived from pooled stomach samples rather than individual stomachs, and (3) the effect of ignoring biological factors that affect the evacuation of prey. Estimating consumption from only two stomach samples yielded results close to the actual intake rate in a simulation study. In contrast to this, a serious positive bias was introduced by estimating food intake from the contents of pooled stomach samples. An expression is given that can be used to correct analytically for this bias. A new method, which takes into account the distribution and evacuation of individual prey types as well as the effect of other food in the stomach on evacuation, is suggested for estimating the intake of separate prey types. Simplifying the estimation by ignoring these factors biased estimates of consumption of individual prey types by up to 150% in a data example.

Paper VI

Functional and aggregative response of North Sea whiting

A. Rindorf and H. Gislason

Journal of Experimental Marine Biology and Ecology, 2005, **324**, 1-19

Abstract

The functional response of whiting (*Merlangius merlangus* L.) to clupeid and gadoid prey was determined from estimates of food intake and prey density at five locations in the North Sea. The intake of most prey types was well described by a type II (decelerating) response, although in some cases a type III (sigmoid) response provided a slightly better fit. Though a saturation level was reached for all types of fish prey, none of the levels corresponded to the maximum digestive capacity of the predator. This was not caused by ingestion of other prey as the amount of other food and fish prey ingested were not negatively correlated. An investigation of the occurrence of fresh fish in the stomachs revealed that fish was ingested almost exclusively during dawn and dusk and the lack of negative correlation between the intake of fish and other prey may thus be a result of the limited time in which fish prey was vulnerable to predation. No aggregative response of the predators was detected towards any of the prey and catches of prey and predators were slightly negatively correlated. There was evidence of an increase in mortality with density at low clupeid densities, but mortality decreased to virtually zero at high densities. Whiting seem therefore unlikely to impose a regulatory effect on their fish prey outside a narrow range of prey densities.

Paper VII

Testing prey selection models in a natural environment: prey selection by whiting

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Abstract

This study presents an investigation of the ability of three different prey selection models to describe the diet composition of large whiting (*Merlangius merlangus*) preying on herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and juvenile whiting. The data consisted of estimates of prey density and predator consumption obtained from trawl catches and predator stomach contents at five locations in the North Sea. The models examined include the two prey selection models on which most population models are based: the multispecies functional response and the switching model. Neither of these models described the data well, as the predator preferred the least abundant prey in most cases. This selection pattern leads to increased mortality on a prey as the density of this prey is decreased. It renders the predator unable to control prey density and enhances natural fluctuations in prey density. The last model examined was a model in which the preference was allowed to change with the condition of the predator. This model provided a remarkable fit to the preference for sprat relative to herring as preference for herring increased with

increasing condition. A similar though less clear result was found when the preference for herring relative to whiting was examined: preference for herring increased with predator condition. According to both optimal foraging theory, the multispecies functional response and the switching model, this relative preference should be unrelated to predator condition.